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## Are Earthworms Important in the Decomposition of Tropical Litter?

*Carlos Fragoso<sup>1</sup> and Patrick Lavelle<sup>2</sup>*

<sup>1</sup> Instituto de Ecología. A.P. 63 C.P. 91000 Xalapa, Veracruz,  
Mexico

<sup>2</sup> Laboratoire d'Ecologie des Sols Tr, Université Paris VI/ORSTOM  
Centre ORSTOM, 72 route d'Aulny 93143 Bondy, France

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The role of earthworms in litter decomposition is well documented for temperate forests (Satchell, 1967; Edwards & Lofty, 1977; Satchell, 1983). In the tropics, however, the information is scarce and limited to a few sites (Madge, 1965; Lavelle, 1978; Lee, 1983; Dash and Patra, 1979). In addressing the question posed in the title of the present paper the following points should be considered: (1) the ecological aspects of tropical earthworm communities (spatio-temporal patterns, diversity and structure), (2) their importance in the macrodecomposer system, (3) their feeding habits and (4) the evidences concerning their direct effect on litter decomposition (litter bag and food selection experiments). The present chapter is an attempt to integrate these aspects and summarize the known effects of the role of earthworms in the decomposition of tropical litter.

### **TROPICAL EARTHWORM COMMUNITIES**

The main natural terrestrial ecosystems in the tropics are forests and savannahs. There are considerable data concerning the ecology of earthworm communities from African savannahs (Lavelle, 1978, 1983a) and from the tropical rain forests of Central America (Fragoso, 1985; Fragoso and Lavelle, 1987), South America (Nemeth, 1981;

Nemeth and Herrera, 1982; Lavelle and Pashanasi, 1989) and Africa (Lavelle, 1978; Montadert, 1985), which provide source material for determining general patterns. In disturbed sites a considerable amount of work has been done in Indian pastures and agricultural systems (e.g. Dash and Patra, 1977; Senapati, 1980). For tropical rainforests, we follow the synthesis made by Fragoso and Lavelle (1992) of 31 communities from 14 different localities; for tropical savannahs the study of Lavelle (1983a) provides the information base.

### Species Richness and Diversity

In tropical rainforests, the number of species for a given community ( $\alpha$  Diversity) varies from 4 to 14, with a mean value of  $6.5 \pm 1.3$  spp; diversity (1/Simpson index) shows a mean value of  $3.6 \pm 0.7$ , ranging from 1.7 to 6.5. At a geographical scale (that is, for communities within a given locality) both species richness and diversity (e.g.  $\beta$  diversity) increase, with mean values of  $10.7$  spp  $\pm 4$  (range of 7–17) and  $4.4 \pm 2.5$  (range of 1.7–8.9) respectively.

In African savannahs the number of species is 4 and 14 spp for Foro Foro and Lamto, respectively whereas in Indian pastures (Senapati, 1980) 5 species have been recorded. Finally, induced pastures of tropical America and the West Indies have low species richness of 2 to 5 species (Lavelle *et al.*, 1981; Barois *et al.*, unpublished data; Fragoso, 1993).

### Abundance and Biomass

Average density and biomass values in tropical rainforests are 68 ind./m<sup>2</sup>  $\pm 32$  (range = 4–401) and 12.9 g/m<sup>2</sup>  $\pm 6.22$  (range = 0.2–71.9), respectively. Within the same locality richer soils support greater densities and biomasses of native earthworms. Maximum densities and biomasses are found in forests in the precipitation range of 2000–4000 mm, indicating that tropical forests with annual rainfall values below 2000 mm are too dry to support high earthworm populations, whereas soil earthworm populations progressively decline where rainfall exceeds 4000 mm. In natural tropical savannahs with annual rainfall of 1000 to 1300 mm, density and biomass values vary in the ranges of 188–582 ind./m<sup>2</sup> and 17–49 g/m<sup>2</sup>, respectively. In tropical pastures induced from tropical forests with higher rainfalls, opportunistic pantropical species e.g. *Pontoscolex corethrurus* or *Polypheretima elongata*, may build up dense populations with biomasses of up 100 g/m<sup>2</sup> (Lavelle and Pashanasi, 1989) reaching maximum values of 360 g/m<sup>2</sup> in rich vertisols of Martinique (Barois *et al.*, unpublished data).

## Spatiotemporal Patterns

*Vertical distributions:* Earthworms of tropical savannahs and tropical rainforests are present throughout the top 40 cm of the soil profile. The average vertical niche overlap (Pianka index, Pianka, 1974) calculated for the tropical forests of San Carlos de Río Negro, Venezuela (0.50, Lavelle, 1983b after Nemeth, 1981), Chajul, Mexico (0.47, Fragoso and Lavelle, 1987) and Dimonika, Congo (0.74, Montadert, 1985) gives a value of 0.57, which is very similar to the mean value of 0.47, calculated for three facies of tropical African savannahs (Lavelle, 1983b). This indicates that tropical earthworms utilize all the food resources available throughout the soil profile. They are found from the deeper soil layers to the hanging soils associated with epiphytes and the crowns of palmtrees.

*Horizontal distributions:* The only detailed study in tropical rainforests was conducted by Fragoso (1985) in the forests of Chajul, Mexico. In that forest, almost all species have aggregated distributions, and this has been mainly explained by variation in soil texture, organic matter and litter quality.

Tropical rainforests of Chajul, Mexico (Fragoso and Lavelle, 1987) and Dimonika, Congo (Montadert, 1985) showed a similar horizontal niche overlap (0.51) that was lower than the values obtained for Amazonian forests and African savannahs (0.70 and 0.69, respectively, quoted in Lavelle, 1983b). This indicates that in tropical rainforests, the greater environmental heterogeneity allows a better niche separation. In these forests, the quantity, quality and timing of leaf litter inputs to the soil system are very important in determining earthworm abundance and distribution, as proposed by Nemeth (1981) and Nemeth and Herrera (1982). These authors consider that differences in earthworm abundance between the lateritic and podzolic soils of Amazonian forests could be explained by the presence of higher polyphenol contents in litter accumulated at the surface of the later soil. The larger amount of polyphenols and other secondary compounds in litter from systems with a poor nutrient status (Janzen, 1985) is thus likely to affect earthworm abundance in tropical forests.

*Temporal distributions:* The pattern of high earthworm abundance and biomass in the wet season, which was found in the forests of Chajul (Fragoso and Lavelle, 1992) and in the savannahs of Lamto (Lavelle, 1978), also occurs in other seasonally tropical forests

(Dimonika, Montadert, 1985; Amazonia, Nemeth, 1981). A more uniform pattern is expected in nonseasonally tropical forests.

### Community Structure

Earthworm communities can be classified in terms of Bouché's categories: epigeic, endogeic and anecic (Bouché, 1972). Epigeics inhabit soil litter and the humus layer. Their main role is to act as efficient agents of comminution and fragmentation of the leaf litter that they transform into stabilized organic matter. Anecics live in the soil and have two main pedological effects: (1) modification of soil structure through the construction of burrows and (2) enhancing the decomposition of plant debris through the burial of leaves (Lavelle, 1988). Endogeic communities, on the other hand, are dominated by worms that live in the soil and that feed on soil organic matter plus dead roots (Lavelle, 1984; Lavelle *et al.*, 1989). These worms have an important impact on the soil structure. They also greatly affect the dynamics of soil organic matter, the main feature being their mutualistic relationship with soil microflora, which gives them the ability to digest low quality organic matter (Barois and Lavelle, 1986; Martin *et al.*, 1987, 1991).

Savannahs are dominated by endogeic communities (Lavelle, 1978, 1983a) whereas tropical rainforests have both geophagus endogeic and detritivore epigeic-anecic communities. Fragoso and Lavelle (1992) in a global analysis of the latter communities concluded that the community structure is mainly determined by soil nutrient contents and rainfall seasonality. In all South American forests and in three African forests the communities are dominated by epigeic-anecics, whereas in all Central American and in one African forest endogeics predominated. The first group was characteristic of oligotrophic soils, in which most nutrients are concentrated in the litter, whereas the second group was typical of rich soils, in which decomposition is faster. Significant relationships between relative abundance and biomass of epigeics and soil litter biomass (Fig. 1) supported these results. It is concluded that the earthworm communities of tropical rainforests have convergent responses towards similar environmental pressures.

In summary, we expect a significant effect on litter decomposition by tropical earthworms in forests with low nutrient status, in which litter appears as the better source of energy. As mentioned later this is often the case.

In those tropical forests and savannahs where soil litter is not a suitable place for living, earthworms have colonized the hanging

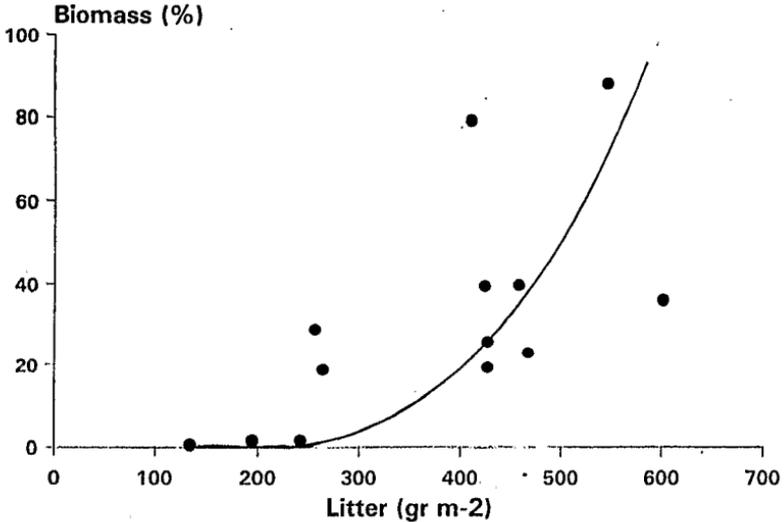


Fig. 1. Relationship between relative biomass of epigeic earthworms and litter accumulated at the soil surface in different tropical rain forests (modified from Fragoso and Lavelle, 1992).

soils of epiphyte bromeliads and palm crowns. In Lamto savannahs, Wasao and Omodeo (1963) and Lavelle (1978, 1983a) found *Dichogaster bolau*, *D. saliens*, *D. baeri*, *D. arboricola* and *Chuniodrilus wattouxi* in litter accumulated in the crowns of several species of palms. In Mexican tropical rain forests Lavelle and Kohlmann (1984), Fragoso (1985) and Fragoso and Lavelle (1987) found *Dichogaster sporadonephra* living in the leaves of the bromeliads *Aechmea mexicana* and *Androlepis skinneri*. Although no experiments have been conducted it is probable that these species affect the decomposition of the litter trapped between the leaves of these plants. In the Amazonian forests, where earthworm communities are dominated by detritivore epigeic-anecics, the worm *Andiorrhinus venezuelanus tarumanis* seasonally climbs to the trunk-canopy area in order to escape flooding (Adis and Righi, 1989). In the same forests Vasconcelos (1990) reported *Oligochaeta* inhabiting the crowns of the palms *Attalea spectabilis* and *Astrocaryum sociale* as a way to extend their normal litter habitat.

#### RELATIVE IMPORTANCE OF EARTHWORMS IN THE TOTAL SOIL MACROFAUNA OF TROPICAL RAINFORESTS

Lavelle and Fragoso (in press), comparing 12 communities from tropical rainforests, have estimated that termites and earthworms are the most important macrofauna of the soil. Earthworms accounted for 51

per cent of total biomass whereas termites contributed 13 per cent; regarding abundance, termites dominated with 37 per cent followed by ants (23 per cent) and earthworms (9 per cent).

There was no relationship between absolute values of density and biomass of termites and earthworms (Fragoso and Lavelle, 1992). When considering relative values a negative relation (either in density or biomass) was obtained that became significant when Mexican forests were excluded. Fragoso and Lavelle explained these results by the fact that in Mexican forests beetles are a very important group that hinders the relationship between termites and earthworms. Finally, the authors conclude that it is not possible to infer that in soils of tropical rainforests earthworms and termites are in competition. More than competitive exclusion, it is the environmental exclusion of one of these two groups that enables the other one to occupy the empty niche.

## FEEDING HABITS

Many studies on the feeding habits of tropical earthworms have been made with geophagous-endogeic earthworms from pastures and savannahs (Lavelle, 1978; Lavelle *et al.*, 1987; Barois, 1987). There are two studies in which the gut contents of epigeics were analysed. In the first case Dash *et al.* (1984) found that a population of *Drawida calebi* (a common inhabitant of Indian pastures) with average biomass of 13.5 g/m<sup>2</sup>, consumes 190,000 m<sup>2</sup> of leaf surface in one year. Kanyonyo (1984) working with the Lamto savanna species *Millsonia lamtoiana* found that the gut content of this species consist of soil (83 per cent), with only a small fraction of organic debris (13 per cent); this last fraction is, in turn, composed by several fractions, the most abundant being grass residues (53 per cent) and seeds (3 per cent).

In tropical rainforests the study of alimentary habits has been focussed on the analysis and quantification of earthworm casts (Madge, 1965; Cook *et al.*, 1980; Nemeth, 1981; Lee, 1983, 1985; Gould *et al.*, 1987). In general it has been found that earthworm casts are richer in organic matter and nutrient contents than the control soil. Average values of cast production are 21 kg/m<sup>2</sup>/yr (Lee, 1983), with maximal values recorded from Malaysian forests (25.6 kg/m<sup>2</sup>/yr, Gould *et al.*, 1987). In this latter study the authors reported the presence of living and dead leaves in the casts of *Pheretima darneliensis* (probably an anecic species). The only study in tropical rainforests with earthworm gut observations was made by Nemeth (1981). This author found in the gizzard of several Amazonian epigeic species (*Andiorrhinus* spp.) leaf debris, densely colonized by fungal hyphae.

These observations explain the positive relationship found between earthworm abundance and soil litter in a spodosol of the same Amazonian forests (Nemeth and Herrera, 1982) (Fig. 2).

### EXPERIMENTAL EVIDENCES OF LITTER FEEDING BY TROPICAL EARTHWORMS

Madge (1965) was the first author who seriously attempted to measure litter consumption by earthworms from tropical forests. The results of that study showed that the eudrilid species *Hiperiodrilus africanus* affects litter decomposition not by pulling leaves into its galleries but by covering them with casts. Anderson *et al.* (1983) working in the forests of Sarawak reported that earthworms did not significantly affect the decomposition of litter placed inside bags of 1 cm mesh size; these and other authors conceded more importance to termites in the decomposition of tropical rainforest plant debris (Golley, 1983; Anderson and Swift, 1983). Swift and Anderson (1989) concluded that the main effect of earthworms is indirect, through the burial of leaves under superficial casts.

### CONCLUSIONS

The present review emphasizes that earthworms are an important component of the total soil macrofauna of tropical rainforests and tropical grasslands. It demonstrates that only in oligotrophic soils of

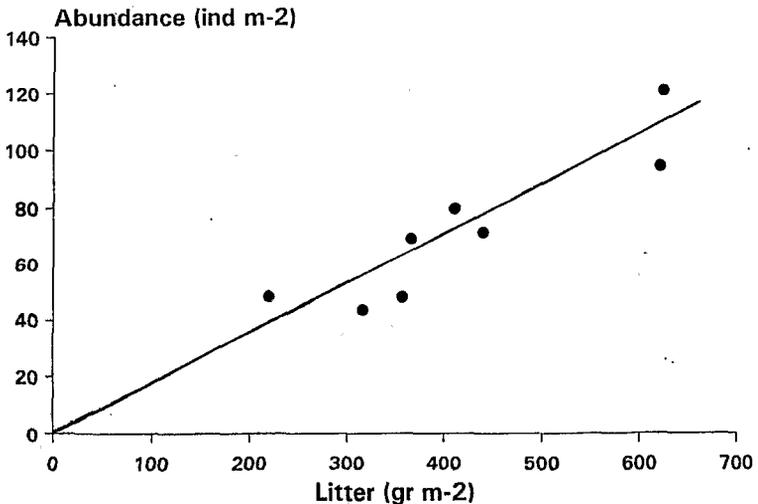


Fig. 2. Relationship between earthworm abundance and soil litter biomass in the tropical rain forest of San Carlos de Río Negro (Amazonian podsol soils) (from Nemeth and Herrera, 1982).

tropical rainforests, dominated by litter-feeding epigeics or anecics, earthworms may have an effect on litter decomposition through a direct consumption. In other forests and in most savannahs, where geophagous endogeics dominate, their effect is indirect through the deposition of casts on litter, thereby enhancing the decomposition process. Polyhumic endogeic species (small unpigmented worms that inhabit the first 5 cm of soil depth; Lavelle, 1983a) which consume the partly decomposed plant debris and humus of the upper layer of soil, also participate in this process. To what extent one of these modalities dominates is currently unknown and requires further research. Experiments of decomposition in litter bags and litter food selection carried out in epigeic-anecic earthworm communities (mainly in South America) could help to test the direct influence of earthworms on litter decomposition. Actually, however, current knowledge points out that earthworms (through the 'drilosphere', the soil system affected by earthworm activities), are more important in the final stages of the decomposition process (e.g., the mixture of soil with the humus fraction) than in the litter system (Lavelle, 1984).

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